Sex-related climate sensitivity of *Araucaria araucana* Patagonian forest-steppe ecotone

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ABSTRACT

Dioecious species offers the possibility to discern plant development in relation to sex. However, there is little information of the incidence of sex on tree-growth sensitivity to seasonal variations in climate. In this study we aim to examine the relationship between the climate and tree growth variability from *Araucaria araucana* inferred from independent male and female tree-ring chronologies derived from old growth forests growing on the xeric environments of NW Patagonia in Argentina. The analysis included 186 standing trees (93 males and 93 females) distributed in five forest stands. After applying a Generalized Linear Mixed Models (GLMMs), result suggests significant differences between tree-ring width related to both sex and climatic conditions. When considering the relationships between tree growth and climate, sensitivity of tree-ring variability to climate appeared to be sex-dependent. While male trees are more sensitive to land precipitation during part of the current growing period, female trees appears to be more sensitive to air surface temperature during the prior period of growth. At atmospheric circulation scales, male trees are more sensitive to the Southern Annular Mode index during the current period of growth. The reported differences in the sensitivity of the response to climate from both male and female trees can be attributed to different mechanisms in the use of the environmental resources. In relation to recent trends in climate experienced in northern Patagonia, these changes, if continued, may compromise the growth and reproductive fitness of the *A. araucana* forests.

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1. Introduction

Dioecy, the phenomenon defined by the presence of male and female flowers on separate plants, represent a relatively small fraction of the total world's flora but have been a focus on the theory of evolution of breeding systems (Bawa, 1980). Although dioecy is considered a rarity in flowering plants, its incidence on the woody species varies, becoming a prominent feature of some regional or taxonomic plant assemblages (Herrera, 1982). For example, dioecy is relatively higher from certain tropical floras comparing with those from temperate climate (Bawa and Opler, 1975). Gynodioecy and monoecy has been distinguished as two principal evolutionary pathways from hermaphroditism to dioecy (Barrett, 2002). Moreover, and under a mechanistic point of view, a sexual selection favoring the evolution of dioecy may be linked to the fact that plants with exceptionally heavy crops or fruit may attract disproportionately many seed disperser (Givnish, 1980).

Independently of the probable links of dioecy to life form, successional stages or habitat type, dioecy is an opportunity for comparisons of a within-species sex-related allocation to test investment resources or growth pattern responses through tree life (Obeso, 2002). The parental-related reproductive (seed production) effort, however, is an aspect where many questions still persist in the discussion forums of plant biologists. To a leaf-level physiological trait dioecious plants express differences between sexes at their photosynthetic capacity, leaf N, water use efficiency, and tissue water relations (Rottenberg, 1998; Dawson and Geber, 1999; Bazzaz et al., 2000; Case and Ashman, 2005). To a whole plant scale, the reproductive cost of growth in dioecious trees may potentially be interpreted through dendrochronological information coupled with long series of reproductive measurements. These data provide a valuable avenue for analyses of time-lagged effects of reproduction, but also for interactions between seed production, tree growth and climate variability (Thomas, 2011).

Although climate-sensitive tree-ring series is a basis for deriving long-term reconstructions of climate history (Esper et al., 2002; D'Arrigo and Wilson, 2006), some bias in this interpretation can be linked to different patterns of resource allocation that

potentially induce sex-specific sensitivity of tree growth to climate (Rozas et al., 2009). Despite this important issue, dioecious species have received little attention regarding the effects of reproduction over growth, as expressed by tree ring characteristics. This is also supported by the reduced set of publications linking sex to tree-growth and sensitivity to climate variations in temperate species (see Silvertown and Dodd, 1999). For example, in *Juniperus thurifera* L. it was observed that growth of male trees react positively to precipitation variability during winter and spring months of the current growth period while female trees correlates positively with current spring precipitation (Montesinos et al., 2006). It was reported, however, that young females of this species are more sensitive to water stress during summer (Rozas et al., 2009). Moreover, in the parental *J. communis* subsp *communis*, Iszkuło and Boratynsky (2011) claimed that growth of female trees is more sensitive to low temperature and low rainfall that in male trees. The growth of *Taxus baccata* L. female trees is negatively correlated with temperature during the prior year but positively correlated with precipitation in the current year (Cedro and Iszkuło, 2011). However, another temperate conifer, such as *Austrocedrus chilensis* (D. Don) Pic. Serm. et Bizarri, do no show statistical differences among growth and climate variability between female and male trees (Rovere et al., 2003; Nuñez et al., 2008). In a single example for the neotropical ombrophilous woodlands of Argentina, Cattaneo et al. (2013) reports that female and male trees of *Araucaria angustifolia* (Bertol.) Kuntze have different growth reactions to variations in both temperature and precipitation.

According to the aforementioned studies, no general pattern of sex-related responses to climate is evident for dioecious plants, a fact probably linked to the particular speciés ecology. In this sense, sex-related differences in sensitivity of tree growth to climate have been argued to be the result from competition for the same resources between reproductive and vegetative growth. Koenig and Knops (1998) showed that male trees use spring rains mainly to develop xylem while female trees use the same abiotic resource to invest in the development of other tree organs, such as reproductive cones. This difference in sensitivity between male and female growth to climate may indicate that they are probably taking different advantages of a resource available in the environment. However, there is evidence indicating growth differences according to sex. For example, Montesinos et al. (2006) claims that the *J. thurifera* male trees invest the available environmental resources during winter and spring for growth and not for reproduction, while for other dioecious species, there is evidence that resource investment in reproductive effort is usually higher in female individuals than in male trees (Lloyd and Webb, 1977; Delph, 1999; Obeso, 2002; Ortiz et al., 2002). This trade-off between growth and reproduction could explain why female and male trees may show differences in their growth sensitivity to climate (Obeso, 2002).

In Patagonia, we have additional opportunities for searching sex-related interactions between tree growth and climate. *A. araucana* (Molina) K. Koch (Araucariaceae), commonly named pehuén, is a dioecious evergreen conifer endemic in temperate forests of south central Argentina and Chile, between 37°20′ and 40°20′ SL and in an altitudinal range between 900 and 1800 m (Roig and Villalba, 2008). The influence of a strong precipitation gradient from the cordillera de los Andes to the Patagonian steppe produce dense and mixed pehuén forests on the eastern slopes of the cordillera while in the transition to the dry steppe, the forest distribution is patchy and monospecific (Veblen, 1982). The pehuén is known to be an old tree, reaching ages surpassing 900 years, particularly in forest patches placed on rocky outcrops and surrounded by the dry Patagonian steppe (LaMarche et al., 1979; Hadad et al., 2015). As indicated by previous reports, the inter-annual variability in the ring widths of *A. araucana* trees reveal a strong dependence to the spring-summer climate conditions during both current and prior period of growth (Villalba et al., 1989; Mundo et al., 2012; Muñoz et al., 2013; Hadad et al., 2015) and at scales of climate forcing it has been observed that growth is lower the higher the spring-summer value of the Southern Annular index (Mundo et al., 2012; Hadad et al., 2015). Moreover, another factor that may have an impact on growth is the incidence of seed production. According to Muñoz Ibañez (1984), the pehuén may reach their sexual maturity when they overcome more than 30 years old. After this, the species produces extraordinary cycles of seeds (masting years) that are dispersed gravimetrically or by vertebrates (Sanguinetti and Kitzberger, 2009). It has been argued that selective forces, like pollination efficiency and/or predator satiation, are linked to these mast episodes with a high regional synchronicity (Sanguinetti and Kitzberger, 2008).

Here, we study the interactions between climate and sex-related tree-growth variability inferred from long-term tree-ring series derived from male and female trees of *A. araucana* trees growing on NW Patagonia in Argentina. The subject of this analysis is supported by the hypothesis that physiological responses related to sex may influence differential interactions between tree growth and climate and this issue, in the context of a climate change scenario, may become relevant in predicting the ecological behavior of these old growth forests according to the sex of trees.

2. Material and methods

2.1. Study area

Five stands of *A. araucana* trees placed on the northwestern Patagonian lands of Argentina were studied (Fig. 1, Table 1). These forests are open stands at the forest-steppe ecotone, growing in a rocky ground with a sandy matrix that provides a well-drained substratum. This particular setting suggests xeric ecological conditions as evidenced by a dry-steppe plant assemblage (Hadad, 2013). The regional climate is characterized by an annual precipitation of ~500 mm, mainly concentrated in winter months (80%), and a mean annual temperature of 12.4 °C, with a mean of 19.8 °C and 5.1 °C of the warmest and the cold months, respectively (Schwerdtfeger, 1976).

2.2. Sampling of tree cores

For each standing tree, between two and three transversal wood cores were taken (with increment borer of $\varnothing$ = 5.1 mm) at breast height to capture potential variability in tree growth around the stem. The total cores at the five sites corresponded to 93 male and 93 female trees (Table 1). In the laboratory, these wood samples were air dried, mounted on wooden supports and sanded with progressive finer sandpapers to highlight the annual tree-ring boundary structure. The growth rings were inspected with a stereomicroscope and dated according to Stokes and Smiley (1968). The calendar age of the growth rings was assigned according to the Schulmańs convention (Schulman, 1956) and ring widths were measured with a Velmex Measuring System (precision = 0.001 mm). Dating accuracy of the resulting ring-width time series were verified within and among trees at each collection site, by synchronizing patterns of wide and narrow growth rings (visual cross-dating through printed graphics; Stokes and Smiley, 1968), and statistically controlled by using the COFECHA software (Holmes, 1983). No missing or false rings were detected.

2.3. Chronology development

The exactly dated raw ring-width data were standardized (detrended) to remove long-term growth trends associated with
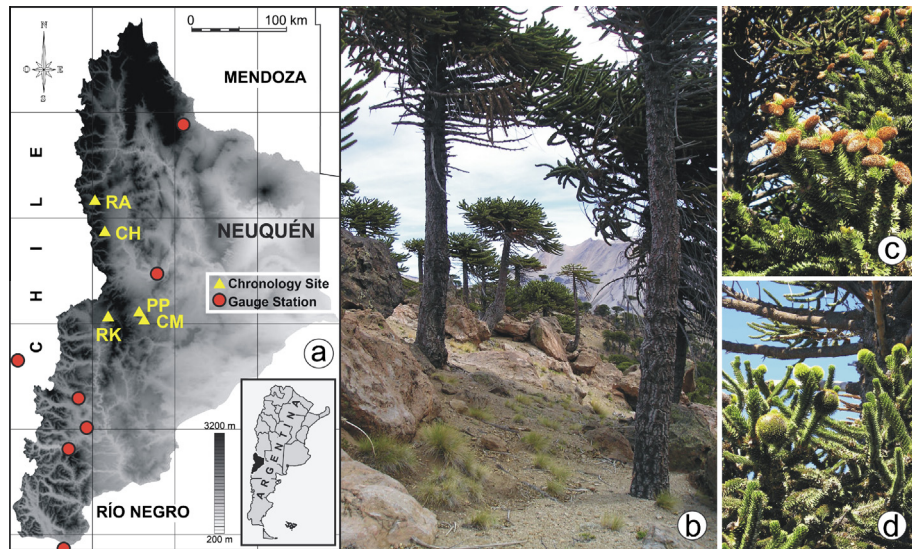
Fig. 1. Location of the study sites in the NW Patagonia Argentina (a; see code of sites in Table 1). Triangle indicates chronology site and circle the gauge stations. Open stands (b) are a characteristic feature of our study sites. Male (c) and female (d) cones are easily distinguished allowing a rapid identification of the tree sex.

the increasing size and age of each individual tree, and to remove differences in absolute growth rate due to local-induced ecological and physiological differences among trees (Fritts, 1976). In this sense, and with the aim to preserve as much as possible the common information in the low-frequency spectrum of each series, we applied the RCS method to standardize series (Briffa et al., 1992; Esper et al., 2003). The software ARSTAN (Cook, 1985) was used to compute the RCS chronology. This procedure implies a construction of a mean regional curve from which we derive a smoothed regional curve necessary to de-trend each of the tree ring series. To construct the mean regional curve we locates the measurements of the width of tree rings all aligned by biological age and calculate the arithmetic mean of the ring width for each biological age. After that, the mean curve is smoothed with a growth curve equivalent to the two third (67%) the length of each tree series. Thus, this smoothed curve is confronted to each of the measured ring-width time series in order to create standardized ring width indices computed by dividing the measured ring-width value for each year by the value of the fitted curve for the same year, producing an index of the tree growth. Finally a robust mean value function is used to compute the mean index chronology to minimize the influence of outliers on the derivation of the mean (Briffa and Melvin, 2011).

The ARSTAN produces three index chronology versions; we used the Residual version, derived from autoregressive modeling

to compute a prewhitened or serially random mean index chronology (Cook, 1985). We apply this procedure to compute the tree-ring width index chronologies for both female and male trees (five chronologies per sex, Fig. 2). After that, and combining separately all measurements by sex, we developed two composite regional chronologies, one for male trees and other for female trees. The quality of the chronology was evaluated using the mean sensitivity (MS), the standard deviation, the average correlation between tree-ring series (RBAR) and the expressed population signal (EPS). The RBAR statistics is the average correlation between all series, which is an expression of the percentage variance in common. The RBAR may change with time as a consequence of changes of the signal strength, which in turn may be caused by differences in the sample size. The EPS statistics (Wigley et al., 1984) is estimated to assess how well a finite-sample chronology compares with the theoretical population chronology based on an infinite number of trees. The EPS strongly depends on the number of trees used in the construction of the mean chronology.

2.4. Meteorological data

For dendroclimatological analyses we considered monthly mean surface air temperature and total precipitation recorded in seven meteorological stations near the sampled sites, but spanning different periods (Table 2, Fig. 1). These climate series were

Table 1
Sample site descriptions and number of trees included in each sex-site chronology.

Site	Code	Latitude S	Longitude W	Altitude (m)	Sex	Number of trees/radii
Río Agrio	RA	37°50′2,6″	70° 58′ 38″	1594	Male Female	29/55 33/63
Chenque-Pehuén	CH	38°05′59,9″	70°52′ 36″	1653	Male Female	20/36 13/18
Primeros Pinos	PP	38°52′ 09,7″	70°34′ 26″	1628	Male Female	16/28 20/38
Río Kilca	RK	38°53′ 53,1″	70°50′ 31″	1442	Male Female	7/13 15/28
Carreri Malal	CM	38°55′ 36″	70°32′ 59″	1510	Male Female	21/37 12/23

Table 2
Meteorological station records used for comparison with tree-ring chronologies.

Station	Latitude S	Longitude W	Altitude (m)	Record Period	Parameter
Buta Ranquil	37°00′	70°07′	1250	1966–2005	T
Las Lajas	38°31′	70°22′	713	1916–1973	T
Flor del Lago	39°20′	72°01′	300	1931–1961	P
Ea. Mamuil Malal	39°39′	71°14′	990	1935–1998	P
Ea. Collun-Co	39° 58′	71° 12′	875	1912–1989	P, T
San Martín de los Andes	40°10′	71°22′	650	1936–1975	P
Bariloche	41°09′	71°16′	825	1951–2009	P, T

P, monthly precipitation; *T*, mean monthly temperature.

inter-compared to determine their degree of similarity ($r = 0.60$) and then averaged to generate a single regional record covering, respectively, the period between 1912 and 2005 for temperature and between 1929 and 2001 for precipitation. In addition, we used monthly data from the Southern Annular Mode (SAM) index covering the period between 1948 and 2002. This index is based on principal components of geodynamic height anomalies at 850 hPa (Thompson and Wallace, 2000). This index represents the variability in the extratropical atmospheric circulation, accounting for ~35% of the variability expressed by the climate of the Southern Hemisphere (Marshall, 2003, 2007). The positive phase of SAM is associated with decreased surface pressure and geopotential heights over Antarctica and a shift poleward and strengthening of westerly winds (Garreaud et al., 2009). It is characterized by persistent water deficit in northern Patagonia during the positive phases, which are associated with a decrease in surface pressure over Antarctica that results in the strengthening and poleward shift of mid-latitude westerlies (Garreaud et al., 2009).

2.5. Ring width data analyses

A Generalized Linear Mixed Models (GLMMs) approach was also used to investigate the potential effects of climate on tree-ring widths. The GLMMs was estimated assuming a *Gaussian* error distribution and an *Identity* link function (Crawley, 2007; Bolker et al., 2009). The ring width was considered as the response variable, sex of individuals as the fixed factor, and sites and stands within sites as random factors. As variables we used those months of precipitation and temperature with the stronger and significant relationship with growth (Mundo et al., 2012; Hadad et al., 2015). The months of precipitation were January of the prior growing period and September of the current period of growth. Whereas for temperature, the months of January, February, and March of the prior period of growth, and the months of October, November and December of the current period of growth were chosen. We used the lmer function from the lme4 package program R (Crawley, 2007), starting with a saturated model until the minimum adequate model obtained through a Hypothesis Testing.
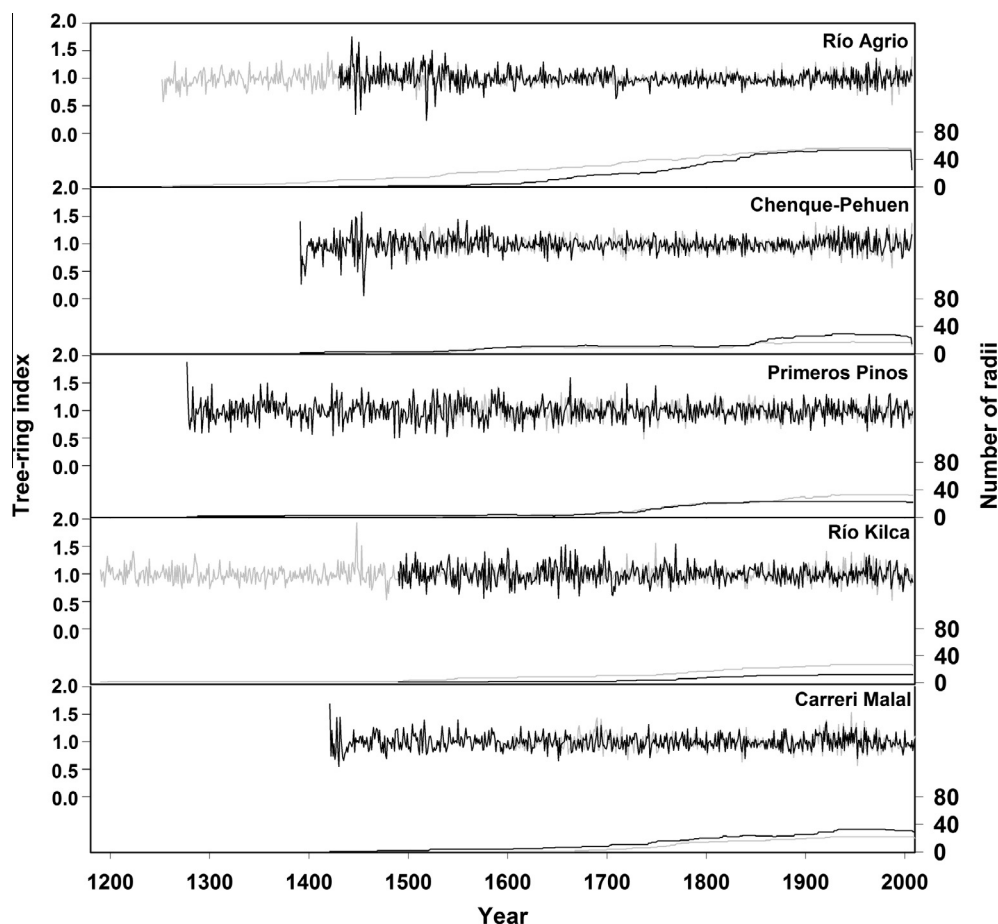

Fig. 2. RCS residual chronologies of female (gray) and male (black) trees of *A. araucana* form the five study sites.

Table 3
Dendrochronological characteristics for the *A. araucana* tree-ring width chronologies.

Site	Sex	Time span	MS	SD	RBAR	EPS
RA	Female	1252–2007	0.134	0.117	0.265	0.860
	Male	1430–2007	0.159	0.148	0.284	0.833
CH	Female	1457–2007	0.143	0.125	0.306	0.788
	Male	1391–2007	0.164	0.155	0.351	0.823
PP	Female	1528–2008	0.175	0.144	0.433	0.884
	Male	1277–2008	0.173	0.152	0.375	0.760
RK	Female	1190–2008	0.143	0.133	0.427	0.810
	Male	1490–2008	0.196	0.169	0.369	0.756
CM	Female	1592–2010	0.143	0.134	0.288	0.808
	Male	1421–2010	0.148	0.136	0.354	0.836

Note: Chronology statistics include mean sensitivity (MS), standard deviation (SD), average correlation between tree-ring series (RBAR) and the expressed population signal (EPS).

2.6. Tree-growth/climate relationships

The relationships between climatic factors and annual growth of *A. araucana* forests were investigated by developing Pearson's correlation coefficients between each tree-ring chronology and the regional climate records previously indicated. The statistical significance of correlation coefficients was considered at the *p*-level of 0.01. Thus, after the correlation analysis, the main climatic

factors influencing tree growth were identified as well as the seasonality and strength of the climate response (Fritts, 1976). Because previous climatic conditions can influence current growth, correlations were performed for each month of a 21-month period to encompass the *Araucaria* growing season.

Finally, spatial correlation patterns at sub-hemispheric scale were identified based on the 850-hPa geopotential height for 20° N–90°S/0°W(E)–160°E(W). These data represents the mean virtual temperature at the referred layer (850-hPa) referenced to Earth's mean sea level, and corresponds, in our analysis, to a 2.5 × 2.5 gridded cells originated from the NCEP re-analysis global dataset (Kalnay et al., 1996). For comparisons with tree growth we used temperature data corresponding to the austral current summer period (December–March) between 1948 and 2010 (data facilitated by National Oceanic and Atmospheric Administration website and the University of Delaware dataset (http://www.esrl.noaa.gov/psd/data/correlation).

3. Results

The statistical properties of the ten tree-ring site chronologies are shown in Table 3. In general, the MS and the standard deviation are greater in male than female chronologies. The mean sensitivity varied between 0.134 and 0.175 (RA and PP respectively) in female trees and between 0.148 and 0.196 (CM and RK respectively) in male trees. The mean RBAR values of female chronologies ranged
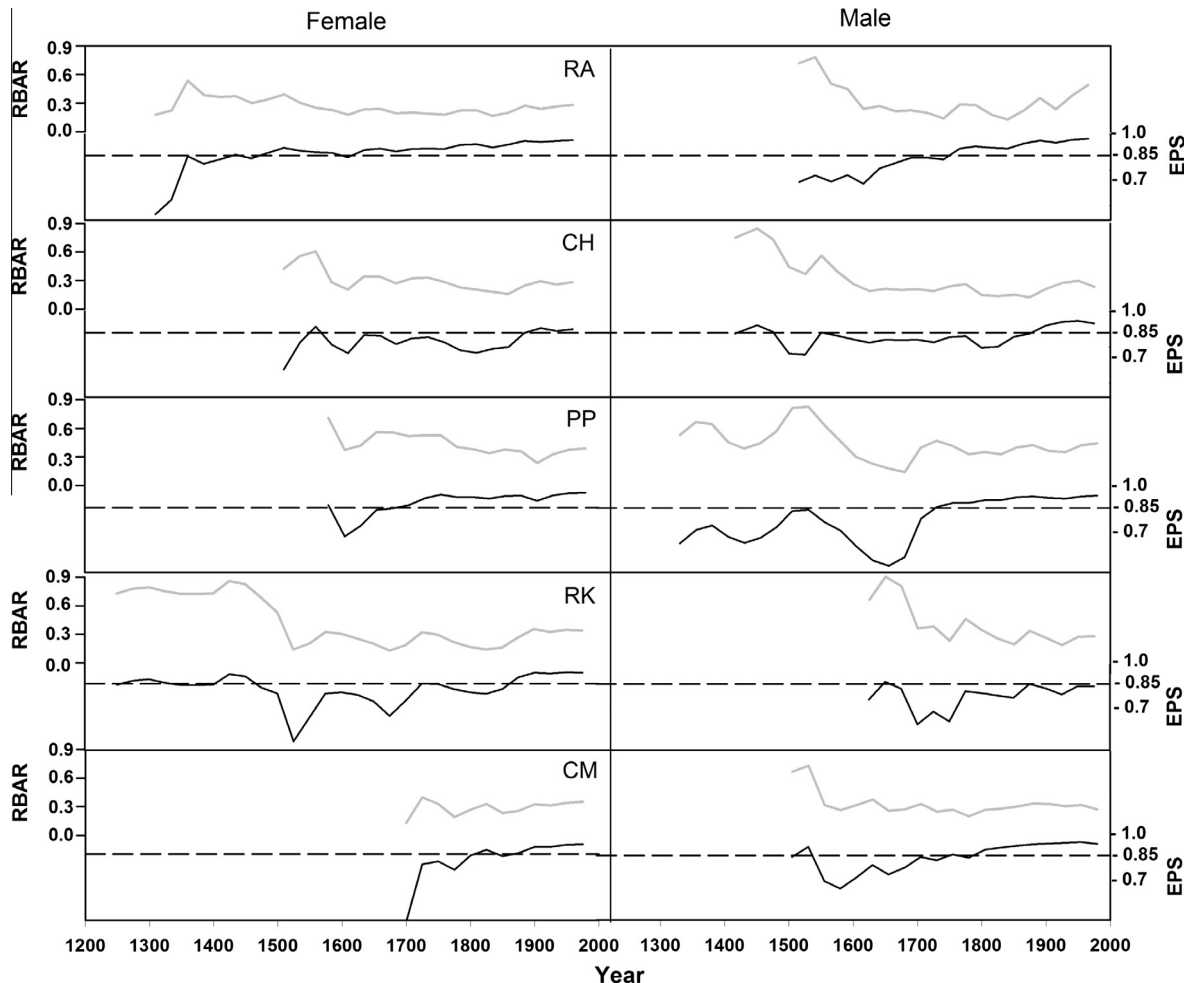

Fig. 3. Average correlation between tree-ring series on (RBAR) and Expressed Population Signal (EPS) statistics, in gray and black respectively, of the residual chronologies *A. araucana* version for each sex by study site.

Table 4
Results of a Generalised Linear Mixed Model (GLMMs), showing the effect of sex of *Araucaria araucana* and climatic variable, and the interaction between sex x climatic variable.

Fixed effects	Estimate	Standard error	*t*-value
Intercept	0.8965096	0.07868578	11.393541[***]
Sex Male regional	0.0624084	0.01125992	5.542527[***]
JanuaryPp	0.0389597	0.00660206	5.901137[***]
SeptemberP	−0.0079142	0.00846248	−0.935215
FebruaryPt	−0.0000325	0.00000645	−5.032306[***]
MarchPt	−0.0000474	0.00000610	−7.763630[***]
OctoberT	−0.0000317	0.00000616	−5.150550[***]
DecemberT	−0.0000229	0.00000602	−3.804997[***]
SexMale x SeptemberP	0.0262959	0.01179395	2.229611[**]

Pp: prior year precipitation; Pt: prior year temperature; P: current year precipitation; T: current year temperature.
[***] $P < 0.001$.
[**] $P < 0.05$.

between 0.265 and 0.433, and for the male chronologies between 0.284 and 0.375 (Table 3). The EPS in all chronologies remains below the 0.85 threshold and exceeded this value in more recent times of the record (Fig. 3). The GLMMs model suggests a significant influence of the tree-ring widths in relation to sex ($p < 0.001$). The precipitation of January and the temperature of February, March, October and December influenced significantly ($p < 0.001$) the tree growth of *A. araucana* in both sexes. Only September precipitation of the current period of male tree growth showed significance at the $p < 0.05$ level (Table 4).

The RCS index for male and female tree-ring chronologies were built with 169 and 170 tree-ring series, respectively. The cambial age RCS ring-width series at both sexes begins around 1.2 mm widths and both male and female series show a negative exponential curve, being this particularly evidenced for the first 100 years, where trees experienced a rapid radial growth (between 0.8 and 1.2 mm) (Fig. 4A). The average growth for female and male trees weighted by the number of series is shown in Fig. 4B. Coincident with the period with the lowest number of trees, both chronologies showed large amplitudes, particularly at periods before the calendar year 1400.

Concerning the climate-tree growth relationship, a similar pattern in the correlation structure was observed for each site chronology when compared with monthly surface air temperature, regardless of gender. As observed in Fig. 5, tree growth was significant ($p < 0.01$) and negatively correlated with temperature during January of the prior growth period at all sites. When compared the regional chronology with temperature, a significant ($p < 0.01$) and negative correlation was evident during January of the prior growth period for both sexes. However, only female trees were significant ($p < 0.01$) and negatively correlated with February of the prior growth period and November of the current period of growth (Fig. 5).

In general, the structure of correlations obtained by comparisons of the tree-ring chronologies with precipitation was similar for all sites (Fig. 6). However, the correlation shown some difference between male and female trees. Female trees from RK and CM sites had significant ($p < 0.01$) and positive correlations during January of the prior growth period. During the current growth period, however, September showed to be positively and significantly ($p < 0.01$) correlated with male tree growth from RA, CH, PP and CM. At the end of the prior growth period (May) the male trees of CH, PP, and RK showed a significant ($p < 0.01$) and positive correlation with precipitation. When comparing rains with the male and female regional chronologies, the month of January of the prior growth period and September of the current growth period appeared to be significant ($p < 0.01$) and positively correlated with male trees (Fig. 6).

When we compared each site chronology with the SAM index, the correlation structure showed a similar pattern to the previously mentioned but with some differences between male and female trees (Fig. 7). Female growth at CH and PP showed a negative and significant correlation ($p < 0.01$) during August, while February of the current growth period was negatively and significantly ($p < 0.01$) correlated with male trees at PP. When male and female regional chronologies are compared with the SAM index, growth linkages with the index appear to be differentially associated in one case to the conditions near to the spring start and in another case toward the end of summer. Thus, there is a negative (although not significant) correlation between female
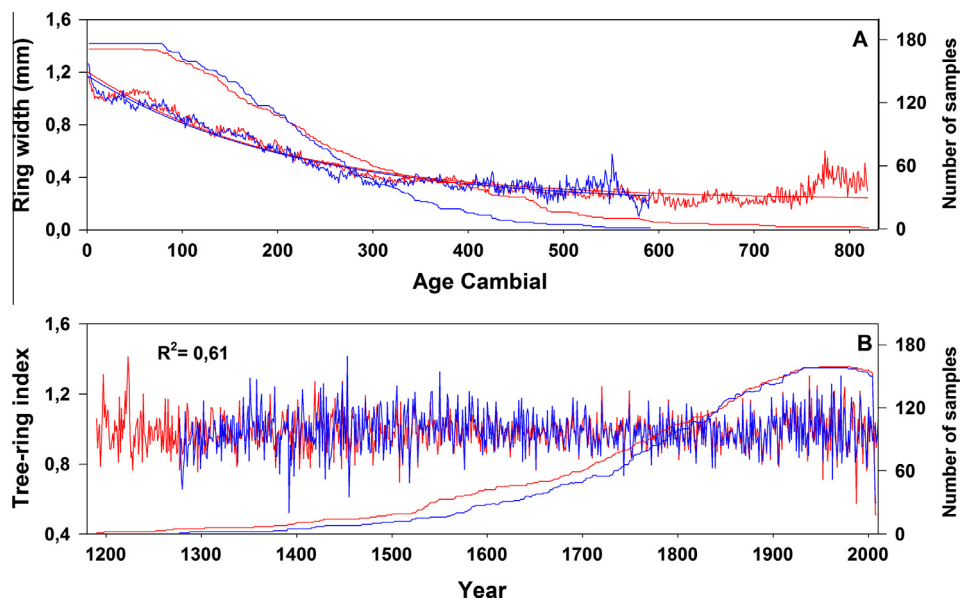

Fig. 4. (A) Growth trends of female and male trees of *A. araucana* of averages of all cores for RCS. (B) Averages of all cores for RCS chronologies from female (red) and male (blue) trees of *A. araucana*. Bottom panels show the replication curves of the male (blue) and female (red) data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
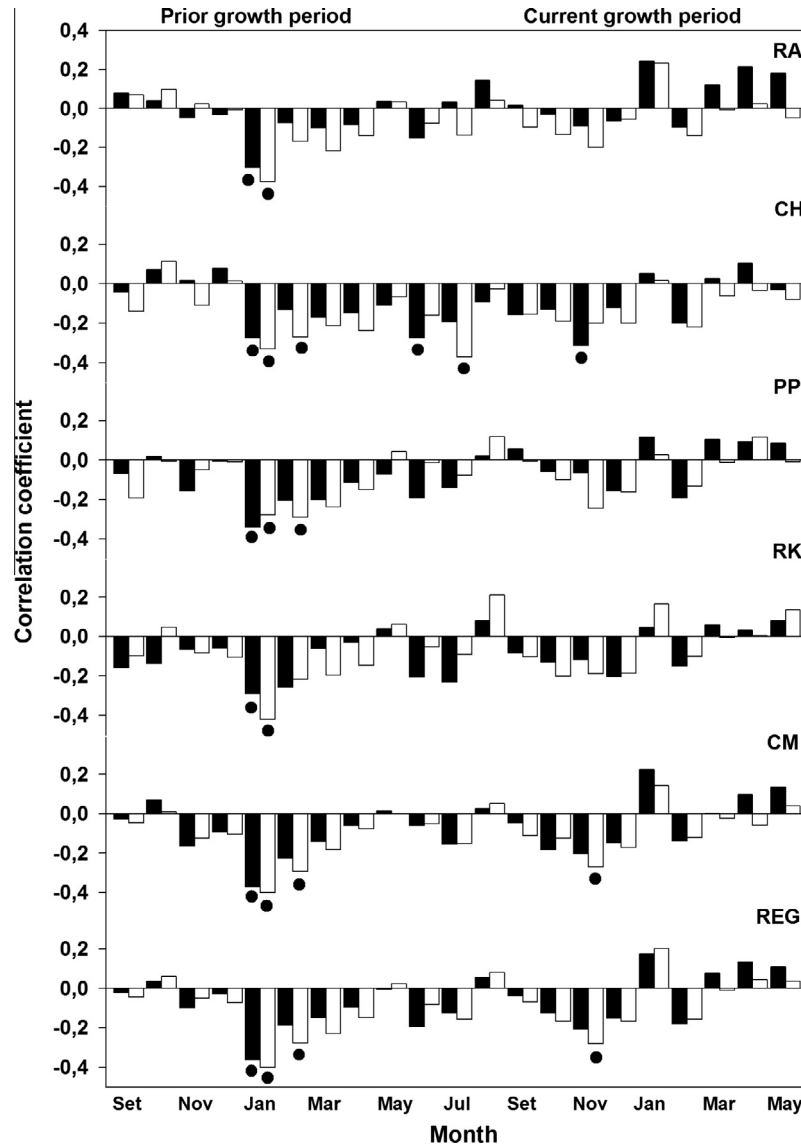
Fig. 5. Correlation coefficients between *A. araucana* RCS chronologies and regional monthly mean land surface temperature (1912–2005). Female (white bars), male (black bars). Black circles indicate the significant level at $p < 0.01$.

growth and August of the current summer while male trees move this association to the summer of the current period of growth (Fig. 7). When we correlated both sex chronologies against the spatial grid of hemispheric temperatures, results showed a different strength relationship according to summer temperatures occurring in both the Pacific Ocean and Antarctica. Although when spatial correlations resulted from comparisons between geopotential height (850 hPa) and the regional chronology of both male and female trees are broadly correlated to summer current (December–March) (Fig. 8A–B), these results are consistent with the previously reported relationship between the tree growth and SAM during the current period of growth. However, in the case of male trees, we observed a more positive relationship with the geopotential height at 850 hPa around the Antarctic region during the current time of growth (Fig. 8B).

4. Discussion and conclusion

Ten long-term tree-ring chronologies developed from 186 trees (93 males and 93 females) provided an appropriate background to record the influence of the local and regional climate variability over the annual growth of trees according to gender. These trees, located in five separate localities along a distance of 120 km in the semiarid lands of the northern Patagonia, represents a particular niche in the ecology of Araucaria, where water is considered a limiting factor that strongly influences the growth expression and natural distribution, being this interaction probably enhanced by specific physiological responses in relation to sex of trees.

Regarding the interaction of xylem productivity among trees, as expressed through long-term inter-annual variability of the growth rings, the GLMMs models showed a significant effect of sex variables on the expression of the *A. araucana* tree growth. Previously, Hadad et al. (2015) applied the same statistical approach in different age class of this tree species though without evaluating the effect of the sex. Regarding the effect of the sex indicated by the GLMMs model, it is possible that there are trade-offs between reproduction and growth. In this sense, there is a recent literature that argues the incidence of an energy expenditure involving gender-specific resource allocation in relation to the reproductive moment, a fact that concern different
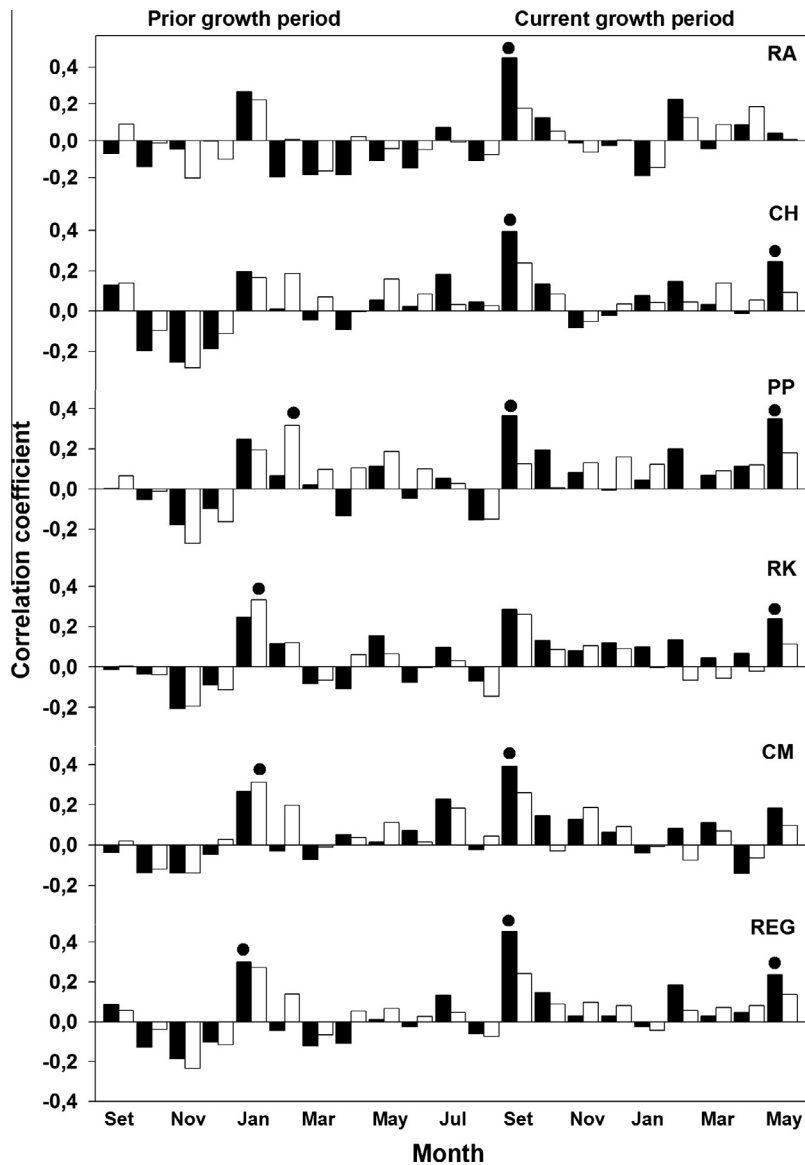
Fig. 6. Correlation coefficients between *A. araucana* RCS chronologies and total monthly regional precipitation (1929–2001). Female (white bars), male (black bars). Black circles indicate the significant level at *p* < 0.01.

trade-offs between reproduction and growth (e.g. Obeso, 2002; Case and Ashman, 2005; Montesinos et al., 2006; Nuñez et al., 2008; Cedro and Iszkuło, 2011). Regarding this concept, a curious cycle of maturation of seeds could be the origin of subtle differences in growth variability in the dioecious *A. araucana* trees. When anemophily occurs between September and October of one year, seed ripening occurs from March to April but of the next growing period. Thus, reproductive cycle of *A. araucaria* take around 18 months from pollination, fertilization of the female gamete, and beginning of the female cone development until seed dispersion (Tortorelli, 1942; Montaldo, 1974). Moreover, this particular construction of the seed in *A. araucana* is coupled with a strong tendency to alternate bearing, producing large amounts of seed every 2–5 years in a perfect regional synchrony (Sanguinetti and Kitzberger, 2008). A possible mechanistic explanation of the regional mast synchrony is the relationship between a large-scale expression of a climate variable (e.j. temperature) and the seed production (Drobyshev et al., 2010). In this sense, Sanguinetti and Kitzberger (2008) claim that pehuén trees produce mast within two years after a drought condition.

The combination of both the environmental site-specific conditions and the plant physiological responses related to sex can, however, potentially interact and influence the tree growth, and this in turn may modulate the sensitivity of radial growth to climate (Rozas et al., 2009), or including, leading to a nonuniform response (Lushuand et al., 2010). Site conditions have been extensively documented as factors that affect the growth of trees (Fritts, 1976), but recent research suggests the possibility that sex in dioecious plants is responsible for a portion of the inter-annual variability of the growth rings (Montesinos et al., 2006; Rozas et al., 2009; Iszkuło and Boratynski, 2011; Olano et al., 2015). Moreover, if reproductive efforts in producing vegetative organs (Leigh et al., 2006; Zunzunegui et al., 2006) imply an influence on the reproduction and development of the meristematic tissue, we may speculate that the curious temporal cone production in *A. araucana*, coupled with a reproductive trait of large seed crops – a masting/intermasting cycle phenomenon (Kelly, 1994), should be considered as a physiological or functional aspect that influences a portion of the growth ring variability and hence be responsible for enhancing sex-specific reactions of tree ring variability to climate.
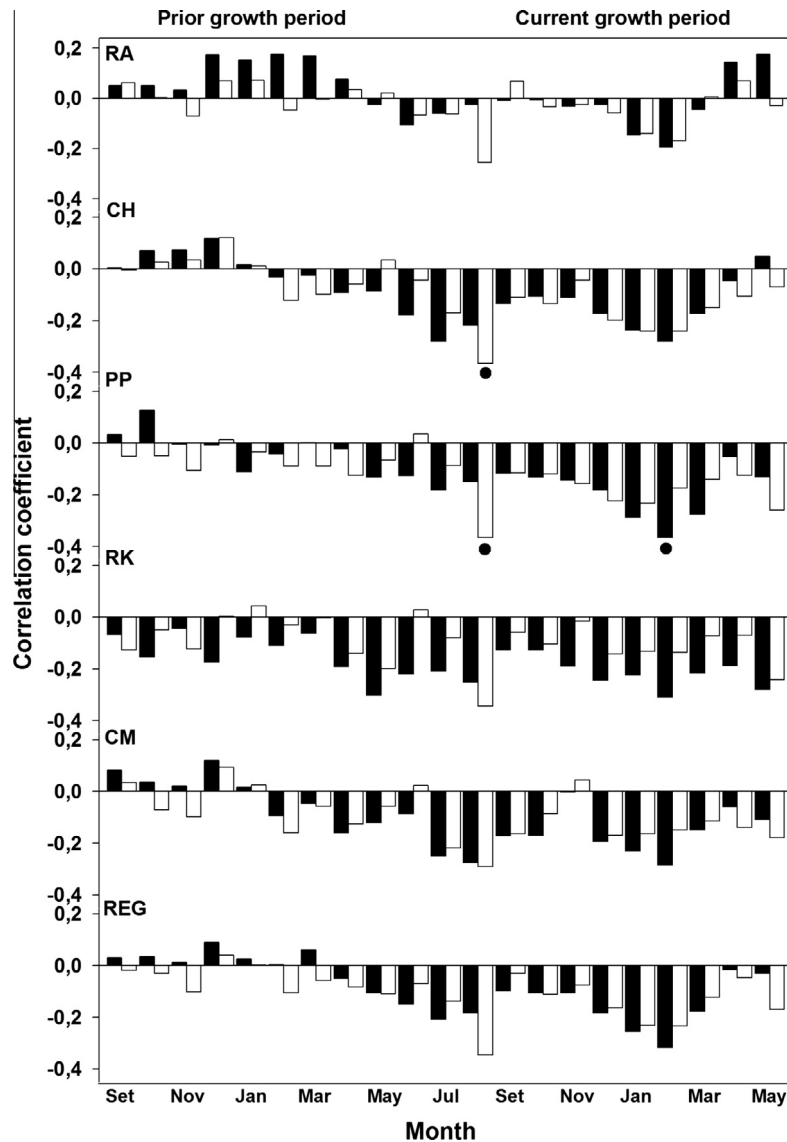
Fig. 7. Correlation coefficients between *A. araucana* RCS chronologies and Southern Annular Mode (1948–2002). Female (white bars), male (black bars). Black circles indicate the significant level at *p* < 0.01.

In this study we have found differences in the tree-growth response of *A. araucana* to climate when growth is separately considered by gender. As indicated in the results section, the inter-annual variability in the ring widths of *A. araucana* trees is inversely related to the variability of the air temperature that occurs in the summer and autumn months of the previous year and during spring of the current period of growth (Villalba et al., 1989; Mundo et al., 2012; Muñoz et al., 2013; Hadad et al., 2015). This climatic signal contained in tree rings is validated by the good fitness observed in the common response of growth to climate, which in turn is consequence of the high common variability between trees, as indicated by the RBAR values for any site analyzed. The present study showed, however, that the ring width sensitivity of *A. araucana* trees to climate variability varies according to sex, evidencing female trees more sensitivity to temperature conditions during the summer before the growth ring formation while September precipitation during the current growing season (Table 4 and Fig. 6) appears to be more related to malés growth.

To extend the sex-related growth/climate comparison to other climate indicators, we considered an atmospheric index representing most of the climatic variability in the Araucaria region. In this sense, we used the Southern Annular Mode (SAM), as a recognized

index that contributes to explain a significant proportion of the Southern Hemisphere climate variability from high-frequency (Baldwin, 2001), through to very low-frequency time scales (Kidson, 1999), and likely responsible to drive the large-scale variability of the Southern Hemisphere (Limpasuvan and Hartmann, 1999; Thompson and Wallace, 2000; Hall and Visbeck, 2002; Marshall, 2003). These comparisons among the SAM and growth indices indicate a similar link to that obtained by using land climate data, and resulting in similar links as reported previously (Mundo et al., 2012; Hadad et al., 2015). Thus, a positive phase of SAM is related to a growth reduction in *A. araucana* during the current period of growth, being this plant reaction explained by precipitation decreases in northern Patagonia during positive phases of SAM at the time of active plant growth (Garreaud et al., 2009; Aravena and Luckman, 2009). However, and as a curious derivation of this study, male trees revealed to be more sensitive to seasonal SAM during the austral current summer, indicating a higher sensitivity to precipitation variability than female trees, a difference that can probably be explained regarding the previously mentioned reproductive behavior for the species.

When these comparisons are performed at a larger geographical scale, there is still evidence of negative correlations between tree
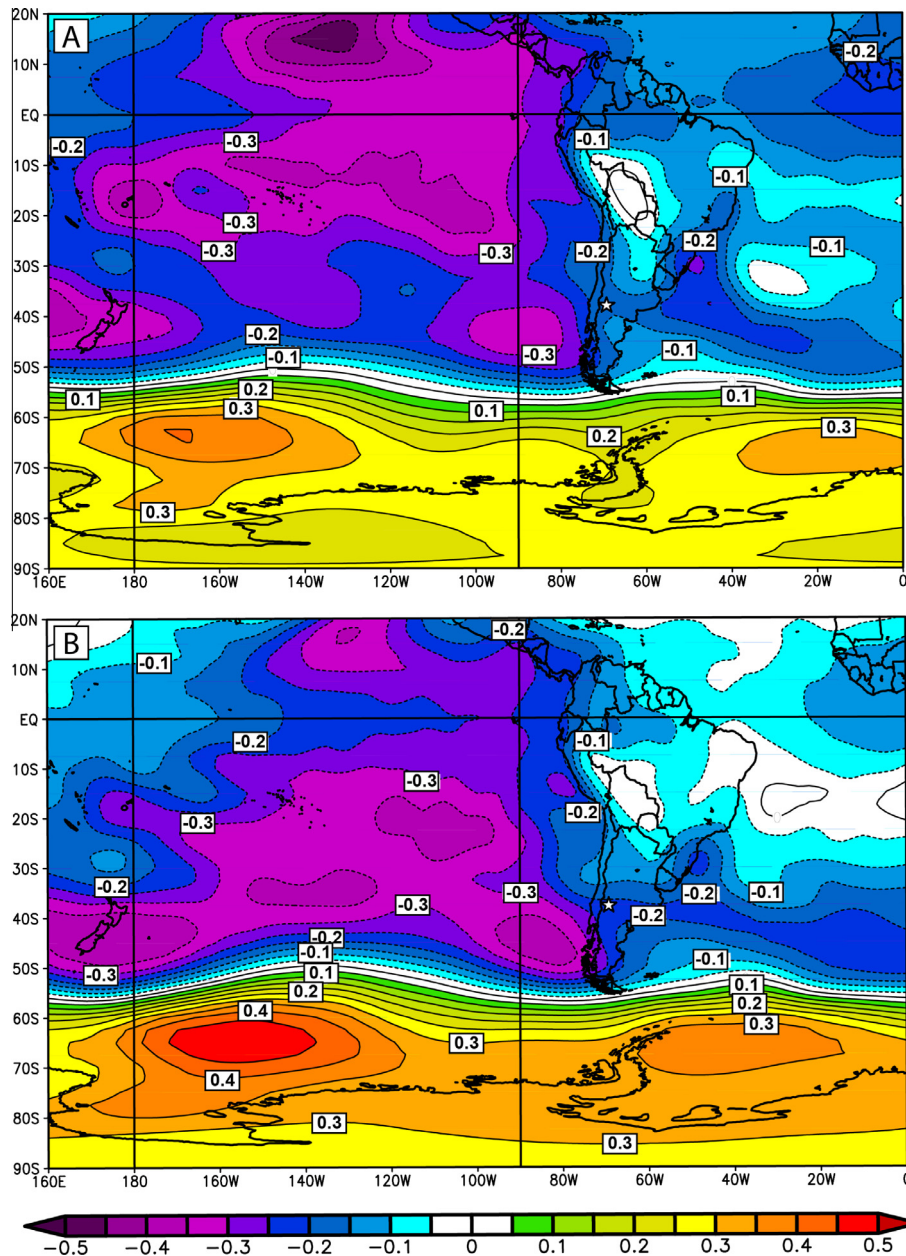
Fig. 8. Spatial correlation patterns from period 1948–2010 between 850-hPa geopotential height and (A) Female tree ring chronology (current period December–March) and (B) Male tree chronology (current period December–March). Data were obtained from the National Oceanic and Atmospheric Administration website (http://www.esrl.noaa.gov/psd/data/correlation/). The location of the 5 study sites are indicates as *white stars*. Significance intervals for *P* > 0.95, are < −0.26 and > 0.26.

growth and the seasonal 850-hPa geopotential height anomalies displayed at the South American sector where the tree-ring chronologies are placed. However, a positive phase is evident when comparing these chronologies with the same geopotential height anomalies occurring around Antarctica (Fig. 8). As the principal mode of variability in the atmospheric circulation of the Southern Hemisphere (SH) extratropics and high latitudes is essentially a zonally symmetric or annular structure, with synchronous anomalies of opposite signs in Antarctica and the midlatitudes (Fig. 8A and B), the detected relationship is consistent with the behavior of the geopotential height over Antarctica in the negative phase of the Southern Hemisphere annular mode (SAM) recorded during last decades (Thompson and Wallace, 2000).

In summary, we showed that when comparing the inter-annual climate variability with the growth of *A. araucana*, differences in the growth-climate sensitivity are evident according to sex.

Considering that during recent decades there has been a positive trend in the SAM activity (Marshall et al., 2011), that these values are unprecedented for the past 600 years (Villalba et al., 2012), and the prediction of future intensification of climate change, including for Patagonia (IPCC, 2007), it is possible to hypothesize an scenario of larger hydric stress where forest dynamics may be influenced by particular responses of trees to climate according to sex, as based on the present results.

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